

## GEOGRAPHIC VARIATION IN SCALATION AND SIZE OF THE BLACK WHIP SNAKES (SQUAMATA: ELAPIDAE: *DEMANSIA VESTIGIATA* COMPLEX): EVIDENCE FOR TWO BROADLY SYMPATRIC SPECIES

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### ABSTRACT

The systematics and nomenclature of the black whip snakes have been the subject of lengthy and complex discussion. Examination of 512 specimens in Australian museums, including type specimens, shows that there are two species in the complex: *Demansia papuensis* (Macleay, 1877) and *D. vestigiata* (de Vis, 1884). When sexual dimorphism is taken into account, they are readily distinguished by scalation, size and to a lesser extent, colour, and are broadly sympatric in northern and north-eastern Australia. The smaller species with fewer ventral and subcaudal scales, *Demansia vestigiata*, is more broadly distributed, reaching south-eastern Queensland and southern coastal New Guinea. Despite the name, *D. papuensis* is not known with certainty from New Guinea.

**KEYWORDS:** Squamata, Elapidae, *Demansia*, Australia, systematics, geographic variation, sexual dimorphism

### INTRODUCTION

Of the Australian elapid fauna, the whip snakes (*Demansia*) remain one of the most taxonomically confusing groups, despite over a century of investigation. Even if one ignores early controversy as to the limits of the genus (Worrell 1961a; Mengden 1983), there has been little agreement on the number of species and the names applied to them. One cause of much of the uncertainty has been a lack of material, with morphologists using small samples, unsure of the relevance of minor differences in coloration and scalation (Storr 1978). One aspect of this confusion has been systematics of the black whip snakes of northern Australia and New Guinea, the largest members of the genus.

Krefft (1869) first recorded large whip snakes with lengths of over a metre, assigning material to two species, *Diemenia psammophis* (Schlegel, 1837) and *Diemenia olivacea* (Gray, 1842) and providing a coloured drawing of the latter.

During the next 15 years, two names were proposed for large whip snakes, *Diemenia papuensis* Macleay, 1877, thought to be

from New Guinea, and *Diemenia atra* Macleay, 1884a, from Ripple Creek, Ingham, north Queensland, although neither description provided comparisons with other taxa.

Boulenger (1896) recognised the same two species of large whip snake as Krefft, placing *D. papuensis* in the synonymy of *D. psammophis*, and *D. atra* tentatively in the synonymy of *D. olivacea*. This nomenclature was largely followed by Kinghorn (1929), who also recognised *atra* as a distinct variety of *D. olivacea*, and provided coloured drawings of each species.

Within the next 30 years, two additional names were synonymised with *D. olivacea*: *Hoplocephalus vestigiatus* de Vis, 1884, by Mack and Gunn (1955) and *Diemenia maculiceps* Boettger, 1898, by Loveridge (1934).

The first large series of large whip snakes (n = 35) was amassed by Thomson (1935) from Cape York, who considered only a single species, *D. olivacea*, was represented. Thomson first applied the common name black whip snake to these snakes, although some authors used the common name spotted-headed snake (Kinghorn 1929; Glauert 1950).

Loveridge (1934, 1949) and Kinghorn (1942) were unable to consistently distinguish whip snake species, and suggested that only a single species with several subspecies was involved. This suggestion was not adopted by most subsequent authors. Glaucert (1950) recognised *D. olivacea* in Western Australia as a distinct species from the Kimberley. Worrell (1952, 1956, 1961a-b, 1963) with the benefit of field experience with whip snakes in sympatry, also recognised *D. olivacea* as a distinct large species, demonstrating osteological differences between it and *D. psammophis* (Worrell 1956). He initially followed Kinghorn in recognising *atra* as a subspecies of *olivacea* from eastern Queensland (Worrell 1952), although later editions of the same work did not recognise subspecies (Worrell 1961b). He was also critical of Boulenger's synonymies, and transferred *D. papuensis* to the synonymy of *D. olivacea*, therefore re-identifying New Guinean populations as *D. olivacea* (Worrell 1961a-b).

These changes in the species name of New Guinean whip snakes were mirrored by Slater's (1956, 1968) alternative treatments, although in both cases he treated the New Guinea populations as a distinct subspecies, *papuensis*, as did Klemmer (1963). McDowell (1967) and Cogger (1971) referred large whip snakes from northern Australia and New Guinea to *Demansia olivacea*, without recognising subspecies.

A new nomenclatural complication was added by Cogger and Lindner (1974), who critically re-examined the identity of *Demansia olivacea* in the light of their collections from the type locality, Port Essington, and concluded that the name should be applied to the much smaller species previously known as *Demansia ornaticeps* (Macleay, 1878). They resurrected *D. atra* from synonymy for the black whip snake in Australia, but applied the name *D. papuensis* to New Guinean *Demansia*, noting the arbitrary nature of this action. Cogger and Lindner reported examining only one specimen of *D. atra* in their study.

Storr (1978) revised the *Demansia* of Western Australia, and examined limited additional material from the Northern Territory and Queensland. He reported a bimodal distribution in ventral and subcaudal scale counts in black whip snakes over a large part of the Kimberley and the Top End of the Northern Territory, and concluded for the first time that two broadly sympatric species were represented. The smaller species he identified as *D. atra*, referring to it specimens from Western Australia, the Northern Territory and Queensland. The larger species he described as *D. papuensis melaena*. In recognising this taxon as distinct, Storr considered *D. papuensis* a New Guinean species. He diagnosed his taxon as subspecifically distinct on the basis of differences in ventral counts and coloration, but did not report examining any specimens of the nominate subspecies. Storr's later comparative data (Storr *et al.* 1986), however, agree closely with Macleay's description of the holotype of *D. papuensis*. Storr also re-identified the specimen previously identified as *D. atra* by Cogger and Lindner (1974) as *D. papuensis melaena*, and noted differences between eastern and western populations of *D. atra*. While Storr's study was a major advance on previous results, it did not take into account the potential for sexual dimorphism, which could result in similar patterns of variation in scalation and size.

Parker (1982) followed Storr's nomenclature in referring New Guinean populations to *D. papuensis*, but suggested that more than one species may be present in New Guinea.

Shine (1980) identified *D. papuensis* from Cape York, from a single ovigerous female with larger eggs than *D. atra* (Shine 1985). Additional records of *D. papuensis* from eastern Australia were provided by Wilson and Knowles (1988) and Ingram and Raven (1991), the former authors assigning this population to the nominate subspecies without providing any supporting evidence. This identification was followed by Ehmann (1992) and Golay (1993), while Wells and Wellington (1985) considered *D. papuensis* to be restricted to New Guinea, and *D.*

*melaena* a distinct Australian species. Storr *et al.* (1986) were more cautious, merely identifying the Cape York population as 'some form' of *D. papuensis*.

In a final nomenclatural twist, Ingram (1990) established that the description of *Hoplocephalus vestigiatus* de Vis just predated that of *Demansia atra*, and hence used the combination *Demansia vestigiatus*, since adopted by Hutchinson (1990) and Golay (1993) as *Demansia vestigiata*, but not by Cogger (1992) and most other subsequent authors, who have continued to use *Demansia atra* as the available name for this taxon.

Thus, in summary, there remain disagreements as to the number of taxa of black whip snakes, their distribution, particularly in eastern Australia, and the nomenclature of the taxa. Few authors have reported examining type specimens. This paper resolves many of these problems by examining for the first time all available specimens in Australian museum collections, including type specimens, taking sexual dimorphism and geographic variation into account.

## MATERIALS AND METHODS

Specimens ( $n = 512$ ) were examined from the following collections: Australian Museum, Sydney (AM); Australian National Wildlife Collection, CSIRO Division of Wildlife Research, Canberra (ANWC); Museum of Victoria, Melbourne (MV); Museum and Art Gallery of the Northern Territory, Darwin (NTM); Queensland Museum, Brisbane (QM); South Australian Museum, Adelaide (SAM); Western Australian Museum, Perth (WAM).

Moderate to large specimens were identified as black whip snakes on size and coloration: consistent lack of a transrostral streak; consistent absence of dark nape bands and dark markings on the chin shields; usually dark venter; usual lack of a dark, pale-edged teardrop marking caudoventral to the eye, and usual presence of either dark caudal edges to the more cranial ventrals or a dark dorsum (Storr 1978). Small individuals, in which the adult coloration

was less developed, were also differentiated from other similar-sized *Demansia* by the proportionally very large eye and immature genital tract.

Where possible, all individuals were sexed by gross examination of gonads (testes or ovaries) and accessory ducts (epididymides or oviducts). The gonads were able to be differentiated even on very small individuals when well preserved. For some females carrying oviductal eggs, length and width of one or more eggs was measured with dial calipers.

Snout-vent length (SVL) was measured against a steel rule (50 cm or 1 m). Ventral and subcaudal scales were counted, using the Dowling method (McDowell 1967). Proportional measurements of head shields of small samples were made with an ocular micrometer on a dissecting microscope, to study claims by Boulenger and Storr of the relevance of scale shape to *Demansia* systematics. Head shield nomenclature follows McDowell (1967).

Simple statistical tests were performed with a hand calculator, while regressions and analysis of covariance were performed with the SYSTAT statistical package. In all analyses of scalation and size, sexes were treated separately. The superscripts \*, \*\*, \*\*\* indicate statistical significance at  $<0.05$ ,  $<0.01$  and  $<0.001$  levels of probability respectively.

## RESULTS

**Ventral scales.** Two largely discrete groups of ventral counts are present in Australia, in both males and females (Table 1). In males, there is no overlap (high counts [group A] 199–228; low counts [group B] 169–191). Among females, there is a similarly bimodal distribution with slightly less separation (Group A 198–222; Group B 167–197), only three individuals having counts between 193 and 199 inclusive. These three individuals are clearly assignable to their respective groups on the basis of subcaudal counts and coloration (see below).

The two groups share a wide longitudinal range (Fig. 1). In both sexes, there is a statistically significant easterly trend,

towards higher values in group A (males: ventrals =  $0.71 \times \text{longitude} + 117.4$ ,  $F_{1,64} = 52.384^{***}$ ; females: ventrals =  $0.46 \times \text{longitude} + 147.8$ ,  $F_{1,57} = 19.199^{***}$ ), and lower values in group B (males: ventrals =  $195.1 - 0.10 \times \text{longitude}$ ,  $F_{1,191} = 4.689^*$ ; females: ventrals =  $253.5 - 0.52 \times \text{longitude}$ ,  $F_{1,78} = 40.383^{***}$ ), resulting in the greatest separation of ventral scale counts in the east (analysis of covariance: slopes: males  $F_{1,255} = 62.849^{***}$ ; females  $F_{1,135} =$

$51.158^{***}$ ). However, within each group, no sharp discontinuity in the longitudinal cline is evident.

In New Guinea and on Torres Strait islands, only values within the range of Australian group B are found (Table 1; Fig. 2).

**Subcaudal scales.** When examined without consideration of locality and ventral count, subcaudals in males show a less distinct bimodal distribution, while females do not show a bimodal distribution, although

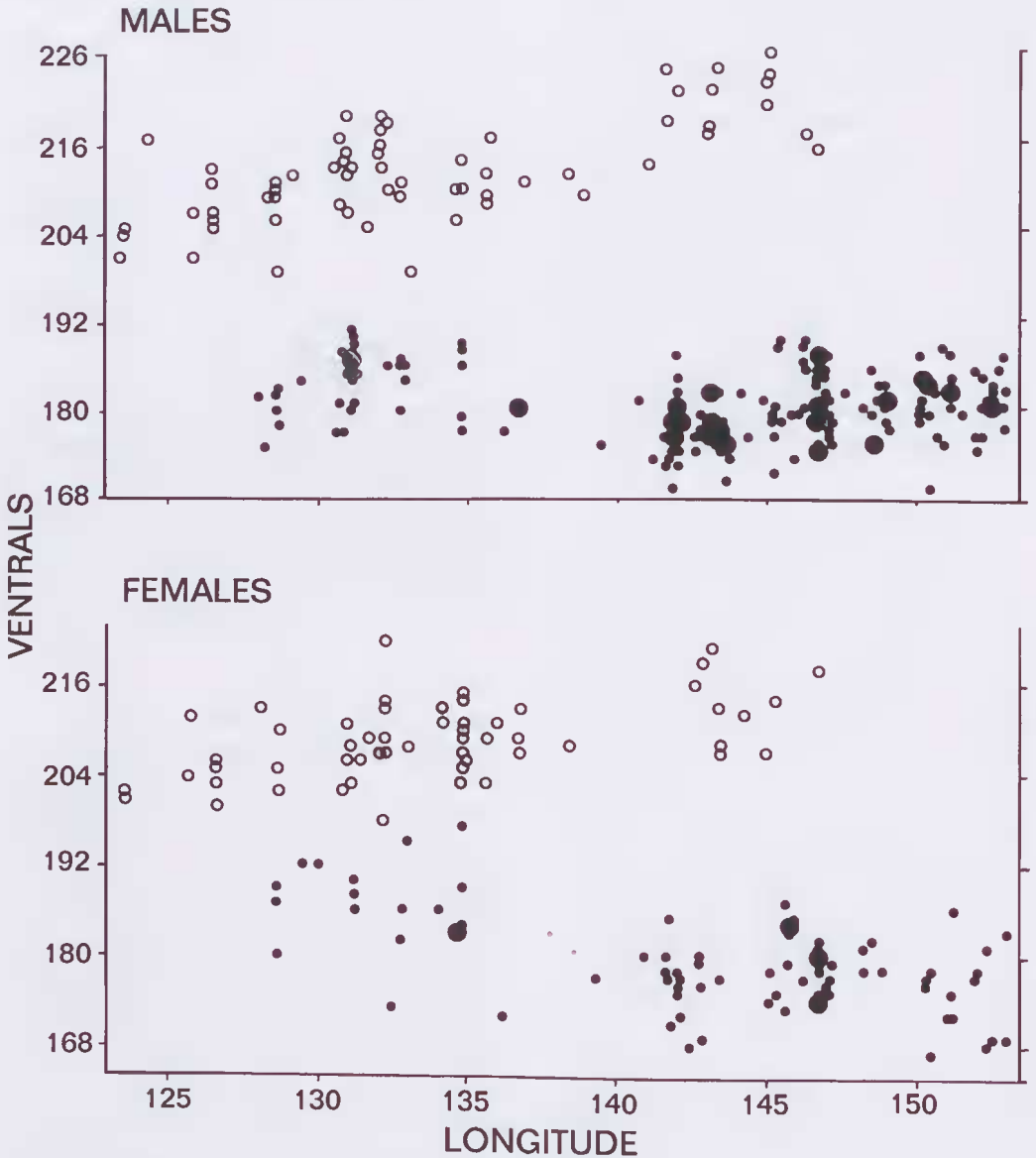


Fig. 1. Longitudinal variation in number of ventral scales in black whip snakes. Open circles are group A, dots are group B. Larger symbols represent multiple data points.



there are several peaks towards the high and low ends of the range. However, when individuals in the two groups of ventral counts are identified, a clear differentiation into two groups of subcaudal counts is obvious (Table 2): animals in group A consistently have high subcaudal counts while animals in group B consistently have low subcaudal counts. The differences between the group means are highly significantly different within sexes (males:  $t_{239} = 20.55^{***}$ ; females:  $t_{126} = 17.14^{***}$ ). Within groups and sexes, there is a statistically significant positive relationship between number of subcaudal and ventral scales (group A: males:  $F_{1,56} = 26.935^{***}$ ; females:  $F_{1,50} = 31.559^{***}$ ; group B: males:  $F_{1,181} = 26.680^{***}$ ; females:  $F_{1,73} = 9.999^{**}$ ).

Again, the greatest distinction between the two groups is in eastern Australia (Fig. 3), and only group B values are found in New Guinea and the Torres Strait islands (Table 2).

**Snout-vent length.** The two groups identified on the basis of scale counts differ noticeably in size, as represented by SVL (Fig. 4). In both groups, males are much longer than females, both in maximum and mean values (group A: males 26.5–154.5 cm,  $n = 69$ ; females 25.9–124.5 cm,  $n = 62$ ;

group B: males 16.4–108.0 cm,  $n = 210$ ; females 19.5–92.6 cm,  $n = 93$ ). The lengths are significantly different between sexes within each group (Wilcoxon Two-Sample Test, group A:  $z = 2.040^*$ ; group B:  $z = 7.124^{***}$ ). Group A animals are significantly longer than group B animals (Wilcoxon Two-Sample Test, males:  $z = 5.079^{***}$ ; females:  $z = 6.867^{***}$ ), with the difference apparent in all parts of the shared distribution, but most obvious in the east, where the largest adults of group A and the smallest adults of group B occur (Fig. 4). It is possible that the apparently larger size of eastern group A animals may be an artifact of collecting, with very large individuals being under-collected in the west. Evidence for this comes from sex ratio data. In group B, males are much more frequently collected than females (ratio 210:93; against a null hypothesis of equality,  $\chi^2 = 44.4^{***}$ ). A non-significant trend towards a male skew is apparent in the Qld sample of group A (17:11;  $\chi^2 = 0.893$ , n.s.), while no clear trend is apparent in the WA and NT sample of group A (50:47;  $\chi^2 = 0.041$ , n.s.). If large animals are under-collected, then the larger males of group A should be collected less commonly than the small males of group B.

**Table 1.** Variation in ventral scale counts of black whip snakes.

	Males				Females				Total (including unsexed)			
	Range	$\bar{x}$	sd	n	Range	$\bar{x}$	sd	n	Range	$\bar{x}$	sd	n
Group A	199–221	213.0	6.80	68	198–222	209.2	5.24	62	198–228	211.3	6.36	137
Group B												
(Australia)	169–191	180.1	4.54	210	167–197	179.3	6.01	92	165–197	179.9	5.11	326
(Torres St)	172–182	178.2	3.77	5	177			1	172–182	178.4	3.31	7
(New Guinea)	174–182	177.6	2.35	12	174–182	177.2	2.78	10	174–182	177.4	2.45	23

**Table 2.** Variation in subcaudal scale counts of black whip snakes.

	Males				Females				Unsexed	
	Range	$\bar{x}$	sd	n	Range	$\bar{x}$	sd	n	Range	n
Group A	80–107	95.9	6.44	58	78–97	87.6	4.96	53	80–105	6
Group B										
(Total)	66–92	80.3	4.52	183	63–86	72.9	4.65	75	63–86	24
(Australia)	66–92	80.4	4.51	162	63–86	72.9	4.27	62	63–86	20
(Torres Strait)	77–83	80.0	3.00	3	80–84			2	80	1
(New Guinea)	70–85	79.5	5.75	11	64–76	70.6	4.00	8	70–75	2

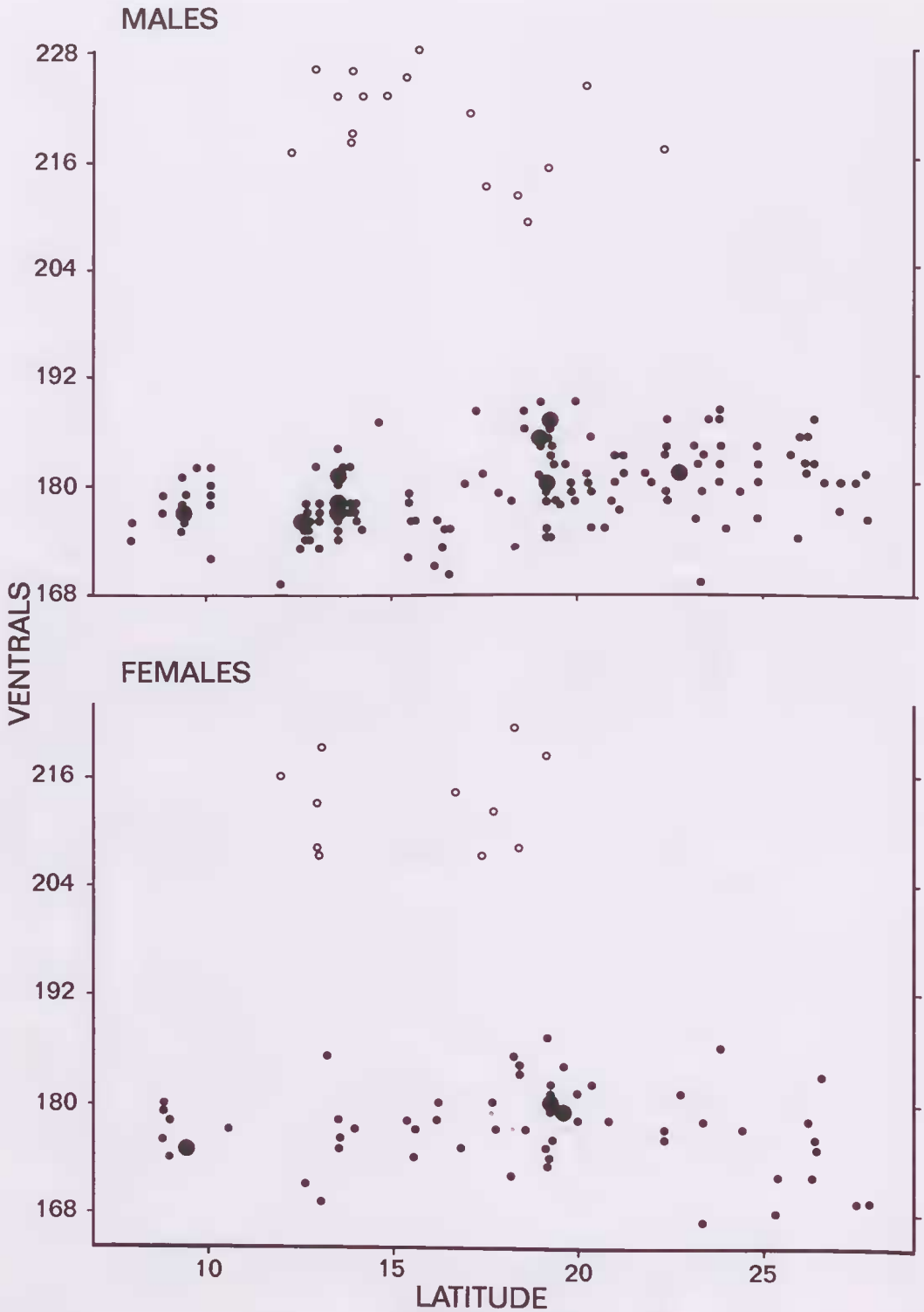


Fig. 2. Latitudinal variation in number of ventral scales in black whip snakes from the east of the distribution (Queensland and New Guinea). Open circles are group A, dots are group B. Larger symbols represent multiple data points.

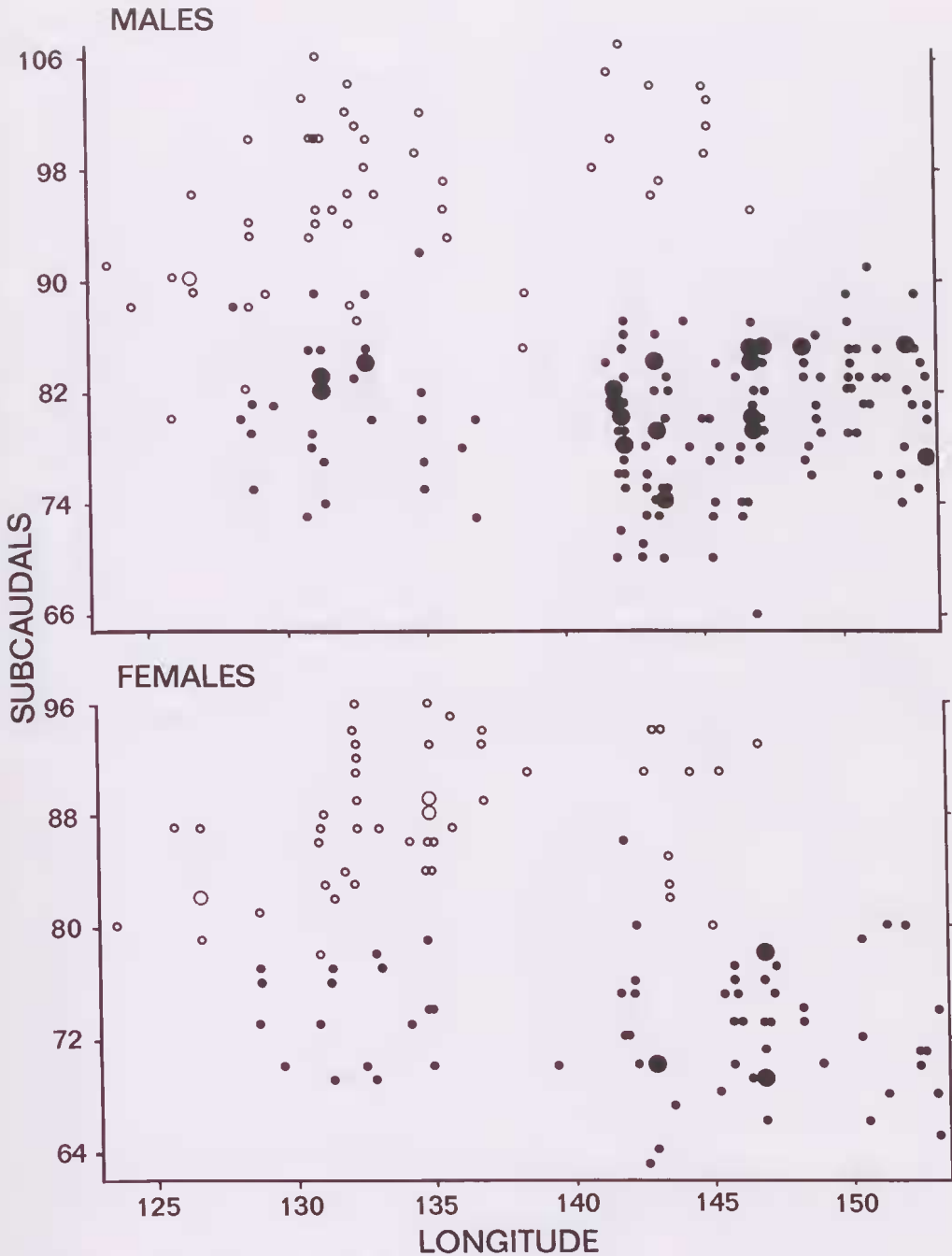


Fig. 3. Longitudinal variation in number of subcaudal scales in black whip snakes. Open circles are group A, dots are group B. Larger symbols represent multiple data points.

The difference in size between group A and B is also apparent at minimum size. The smallest (unsexable) individual of group A has SVL 22.8 cm, while 16 individuals of group B are shorter, with SVL as low as 16.4 cm.

An estimate of size at maturity is available for females from the smallest reproductively active female. For group A, the smallest of 18 females with oviductal eggs or enlarged ovarian follicles has SVL = 78.5 cm, while

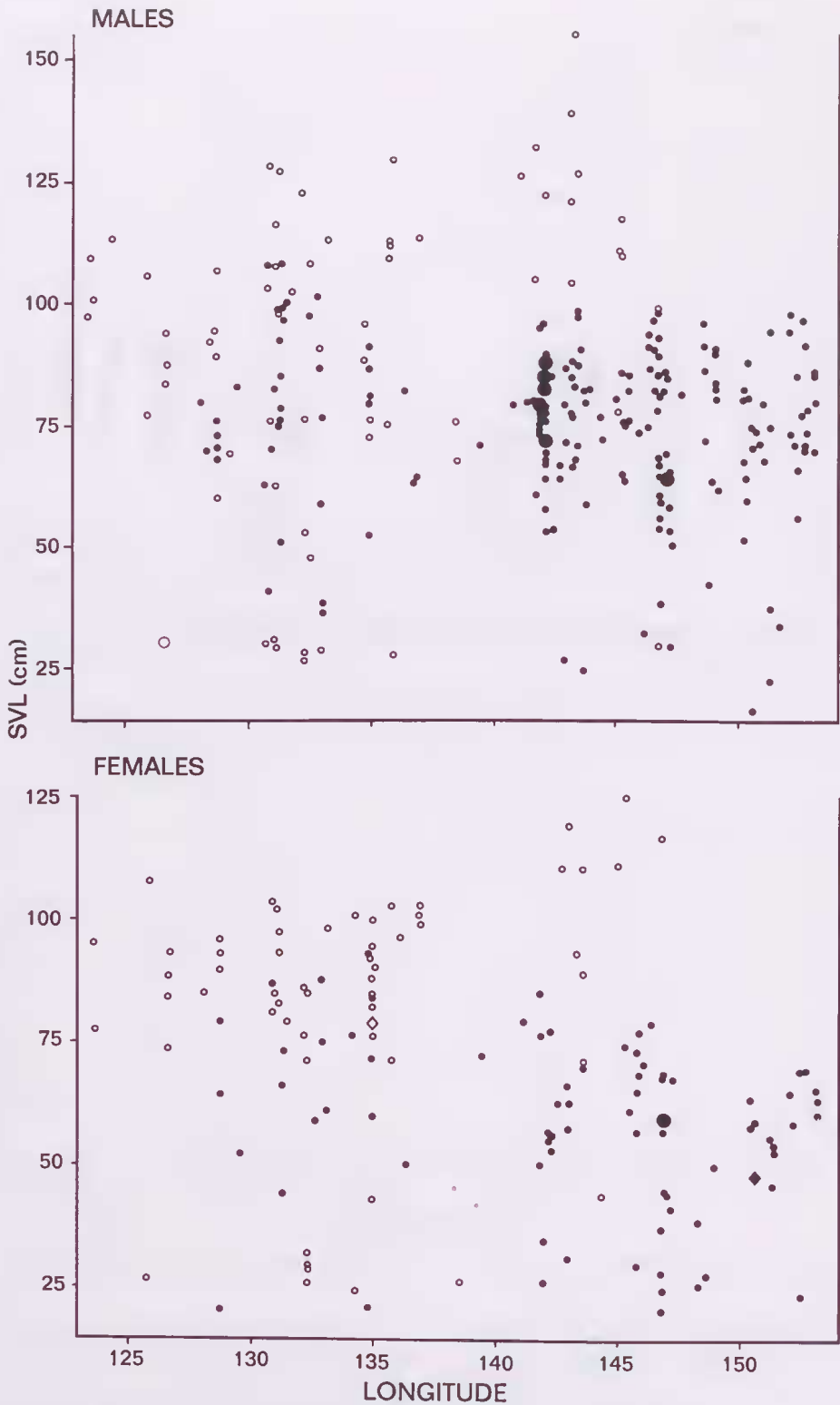


Fig. 4. Longitudinal variation in snout-vent length in black whip snakes. Open circles are group A, dots are group B. Larger symbols represent multiple data points. Open and closed diamonds indicate the smallest reproductively-active females in each group.



in group B, nine reproductive females have SVL from 47.8 to 78.7 cm.

The New Guinea specimens examined are all small, with the largest of the 23 measureable snakes (AM R86833, male) having SVL = 80.8 cm. Parker (1982) records maximum total length for individuals in the Western District as about 1 m, and reports a gravid female from this area with total length = 51.1 cm.

**Coloration.** Coloration differences between groups A and B are apparent, but not completely exclusive of each group.

Group A adults usually have a tan head, often with varying numbers of small dark spots or flecks, both dorsally and laterally. In some individuals, the spots are enlarged, in extreme cases merging to produce a coarse variegation over the head (e.g., NTM R16624). The orbit usually has a narrow, indistinct, broken pale margin. Cephalic markings in group B adults consist of varying expression of moderate to large dark blotches on the dorsal head shields, most extensive in eastern populations, a similarly broken narrow pale rim to the orbit, and often dark apical margins to scales in the temporal region. Some individuals have a short dark 'teardrop' marking caudoventral to the orbit, but not reaching the oral margin. The throat in both forms is immaculate.

Differences between adults of the two groups are also apparent in dorsal markings. In many group A adults, the dorsum is uniform, either dark slate to black (most western individuals, and some eastern individuals) or, less commonly, a lighter brown. Some individuals have dark bases to dorsal and lateral scales, particularly on the nape, but rarely dark apices. In most group B adults, the dorsal and lateral scales on the neck have dark apices, while the more caudal dorsal and lateral body scales are either evenly dark, or have dark bases. Geographic variation in the intensity of the dark markings on body scales is apparent, with many (but not all) adults from the extreme south-east, beyond the range of group A, having only dark bases to otherwise greenish dorsal and lateral scales. In both groups, the tail and caudal third of the body is often red-brown.

In group A, the ventral scales of the throat are usually cream, although some very large adults have traces of dark markings along the caudal margins of the scales. The ventral scales on the body are variably pigmented, from large dark blotches, often laterally positioned, to uniform dark pigmentation. All adults of group B have a well-defined dark caudal edge to the cranialmost ventral scales, which are usually yellow, while the more caudal ventral scales are generally uniformly dark (occasionally ventrals dark only laterally, e.g., QM J44971). In both groups, the tail venter is usually pale, with variable dark blotchy pigmentation.

Both groups show ontogenetic shifts in coloration, with juveniles uniformly pale green-brown and immaculate.

Both groups possess well-defined pale rectangular bars on the craniodorsal and cranioventral margins of body scales of all rows but the most ventral, concealed when the scales overlap, but exposed when the skin is stretched. The bar on the craniodorsal margin is shorter than its partner. The skin between the scales is also pale. These concealed markings are present throughout the genus (Storr 1978).

**Egg size.** From group A, single representative shelled eggs were measured from five ovigerous females (QM J8122, J50555, MV DT-D86, DT-D117, DT-D133) and a full clutch of eight eggs from one female (WAM R74045). The five former eggs have lengths and widths 48.2x17.2 mm, 28.6x13.0 mm, 52.5x11.7 mm, 30.0x14.1 mm and 30.5x12.2 mm (width/length ratio 0.223–0.470). The eight latter eggs have length 35.2–42.9 mm ( $\bar{x}$  = 40.3,  $sd$  = 3.39) and width 13.1–16.5 mm ( $\bar{x}$  = 15.3,  $sd$  = 1.09), with width/length ratio of 0.308–0.469 ( $\bar{x}$  = 0.383,  $sd$  = 0.051).

From group B, two full clutches of eight eggs (NTM R3433, WAM R74045) were measured. The former clutch has length 26.0–35.5 mm ( $\bar{x}$  = 29.5,  $sd$  = 2.89), width 10.0–12.0 mm ( $\bar{x}$  = 11.6,  $sd$  = 0.68), and width/length ratio 0.338–0.462 ( $\bar{x}$  = 0.394,  $sd$  = 0.036), while the latter has length 26.7–32.6 mm ( $\bar{x}$  = 29.2,  $sd$  = 1.85), width 14.4–17.5 mm ( $\bar{x}$  = 16.5,  $sd$  = 0.939) and width/length ratio 0.515–0.616 ( $\bar{x}$  = 0.567,  $sd$  = 0.033).

Thus, while widths of eggs are similar in the two groups, some group A eggs are considerably longer than group B eggs.

**Head scalation.** Head scalation shows minimal variation. What variation is present is apparently due to individual anomalies. In samples of 20 individuals from each of the two groups, representing all parts of the geographic range, the following scalational features occur at least unilaterally on 90% or more of each: rostral about as tall as wide, triangular when viewed from in front; internasals in broad contact, nearly square or a little broader than long; prefrontals in broad contact, longer than broad and longer than internasals; supraoculars about twice as long as broad, about as broad as frontal; each parietal bordered by two temporals and four to five occipitals, the rostralmost occipital largest; nasal completely divided by a large nostril, the two resulting segments about the same length, but rostral part much taller, both segments contacting internasal, caudal segment contacting prefrontal; preocular taller than long, with a prominent canthus rostralis in adults, contacting nasal, prefrontal and supraocular; postoculars two, about equal in size, dorsal postocular contacting supraocular, parietal and primary temporal, ventral postocular contacting primary temporal and supralabials; primary temporal single; secondary temporals between parietal and last supralabial two, lowermost overlapping last supralabial; temporolabial distinct (not fused to last supralabial, *contra* the illustrations of Storr *et al.* 1986), large, deeply wedged between last two supralabials, and narrowly separated from lip; supralabials six, first contacting rostral and nasal, second contacting nasal and preocular, third contacting preocular and entering orbit, fourth entering orbit and contacting lower postocular, fifth contacting lower postocular, primary temporal and temporolabial, sixth contacting temporolabial and lower secondary temporal; caudalmost extremity of fifth supralabial occasionally split off to form a small additional supralabial; infralabials seven, first pair oblique, in broad contact at the mental groove, second pair small, squarish, separated by pregenials; pregenials shorter than postgenials.

The most common deviations from this pattern are extension of the lower postocular to contact the parietal, and extension of the temporolabial to contact the postoculars rostrally or the oral margin ventrally.

Length and width of the frontal shield were measured on slightly larger samples. In 35 specimens of group A, the width/length ratio is 0.416–0.612 ( $\bar{x}$  = 0.491,  $sd$  = 0.041), while in 137 specimens of group B, it is 0.382–0.595 ( $\bar{x}$  = 0.490,  $sd$  = 0.041).

**Distribution and sympatry.** There is broad geographic overlap in tropical Australia between the two groups (Fig. 5), although group A extends generally further inland and west. Group B is more strictly coastal, and extends further to the south-east. Both forms are found together at a number of localities, with the largest samples from Milngimbi Mission, in the Crocodile Islands ( $n$  = 11 in group A, 8 in group B), the lower Archer River, in Cape York ( $n$  = 1 in group A, 15 in group B), and Townsville (including the suburbs Cranbrook, Mudginburra, Gulliver and Pallarenda and James Cook University:  $n$  = 2 in group A, 21 in group B). At each of these three localities, the distinction between the two groups in counts, size and coloration is maintained. Among group B in Australia, one locality is considered erroneous, and another suspect. SAM R1102 is purportedly from 'Minnie Downs', Qld, presumably the station of that name in south-western Qld, very distant from other localities. Given the lack of confirmatory records from this region, I ignore this record. QM J37052 has the locality 'west of Anakie, Qld'. This is further inland than other records at this latitude, and given the imprecise locality, is possibly in error or based on a transported specimen.

In New Guinea, where only group B is definitely recorded, all specimens but one are from the south side of the central cordillera (Fig. 6), and from close to the coast in two regions: the Fly River delta and around Port Moresby. The exception is ANWC R1014, a head and tail from Maprik (East Sepik district). Until confirmatory records are available from this region, I regard this locality as erroneous.

Both forms occur on several offshore islands. Group A occurs on Bathurst and Milngimbi Islands along the Northern

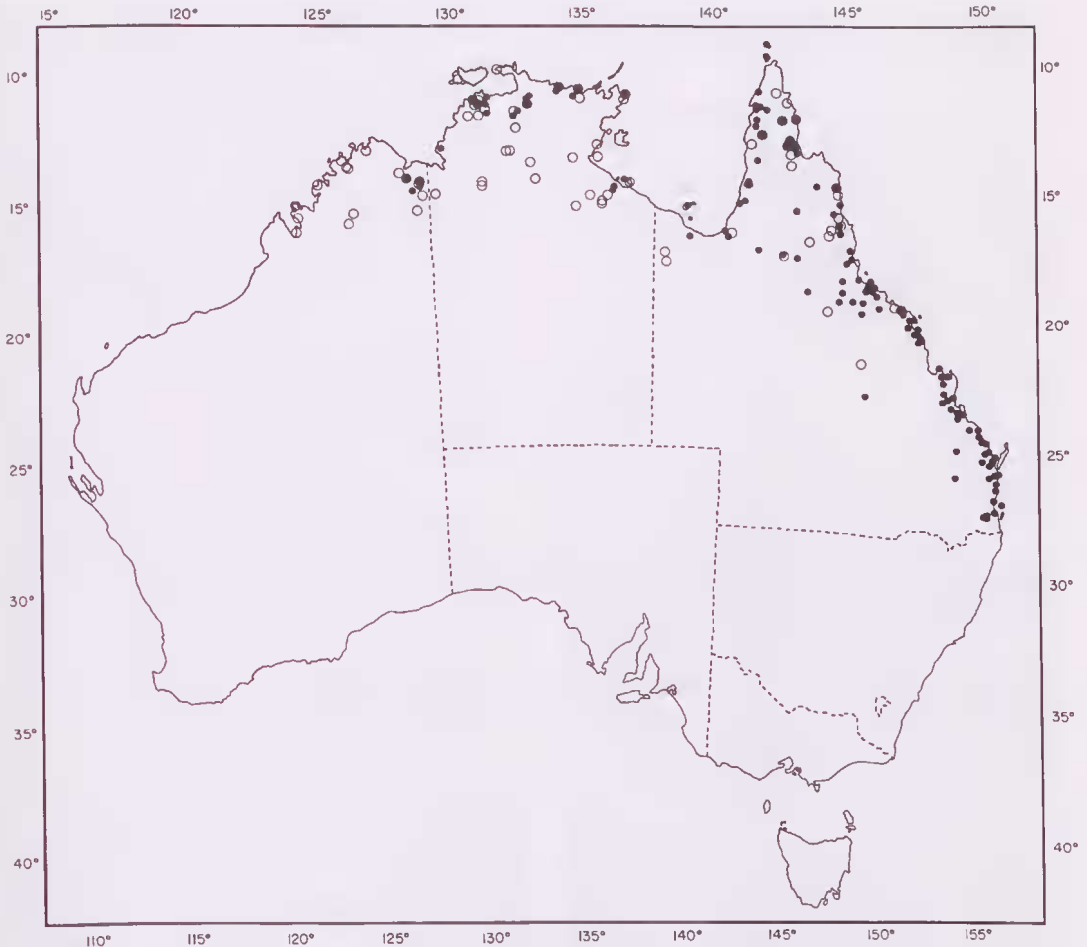


Fig. 5. Distribution of black whip snakes in Australia. Open circles are group A (*D. papuensis*), dots are group B (*D. vestigiata*).

Territory north coast, and Vanderlin and Maria Islands in the south of the Gulf of Carpentaria. Group B occurs on Badu and Thursday Islands in Torres Strait, Milingimbi Island along the Arafura Sea coastline, Centre and Mornington Islands in the south of the Gulf of Carpentaria, and Magnetic, Rabbit and North Stradbroke Islands along the Queensland east coast.

**Type specimens.** *Diemenia papuensis* was described by Macleay (1877) from a single specimen. There is some doubt about the type locality. Macleay (1877) stated that the specimen was simply labelled New Guinca, and suggested that it was collected at Hall Sound by the *Chevert* Expedition. The locality Hall Sound has since been

considered the type locality by most authors (Goldman *et al.* 1969; Cogger 1979; Cogger *et al.* 1983). The holotype (AM R31919, male; formerly Macleay Museum R713; Figs. 7, 8A) is in poor condition, soft and very faded (based on Macleay's description of a much darker coloration and traces of darker tint in non-exposed areas), missing much of the stratum corneum of the scales, and with the vertebral column broken at midbody. It has 222 ventrals, is missing the tail tip, but has 88 subcaudals up to the missing portion, and SVL 129.0 cm (Macleay gives 225 'abdominals', 88 subcaudals, and SVL 51 inches). The left postgenial is malformed, either developmentally or through injury, and the



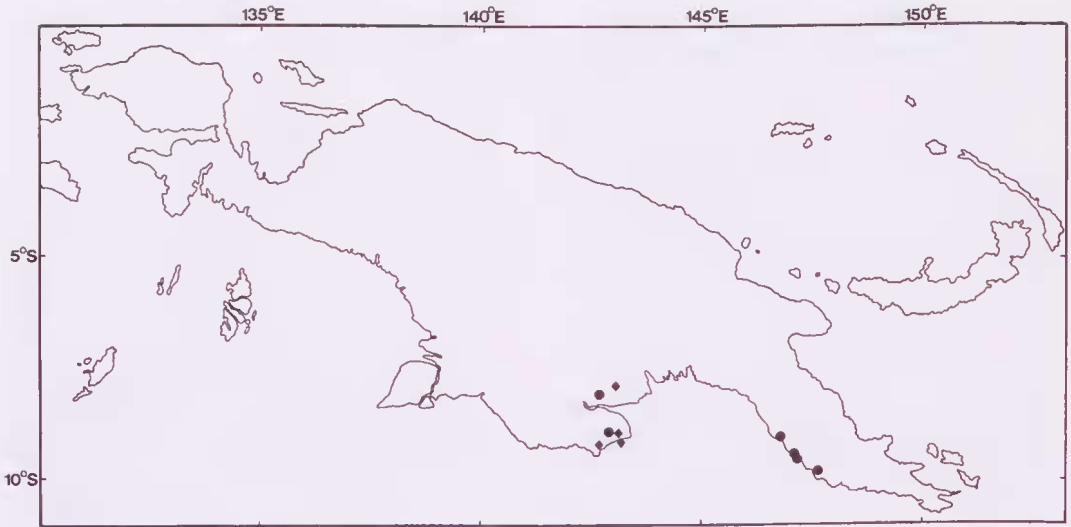


Fig. 6. Distribution of group B black whip snakes (*D. vestigiata*) in New Guinea. Dots are specimens examined; diamonds indicate additional localities cited by Parker (1982).

nasal is narrowly separated from the preocular. On the basis of size and ventral scale count, and the relatively large number of subcaudals, it is clearly referable to group A. However, this form is not otherwise known from New Guinea. Given the lack of precision of the type locality, the fact that the *Chevert* Expedition also collected at two Australian mainland localities (Cape Grenville and Somerset), and that the Macleay collection, during the period preceding Macleay's paper, received other collections from both Cape York Peninsula and New Guinea (Macleay 1875; Tilbrook 1992; S. Norrington, pers. comm.), I believe it likely that the recorded type locality is incorrect.

*Hoplocephalus vestigiatus* de Vis, 1884, was described from a damaged specimen from an unknown locality. The original description gives 152 ventrals, but lacks a subcaudal count and measurements. Corrections to the description were presented by Mack and Gunn (1955), who give 182 ventrals. The holotype, QM J206 (Figs 8B, 9), is soft, lacks large patches of stratum corneum on head and body, with some of the exposed areas dried and distorted, has the throat torn, and is missing much of the tail. It has 184 ventrals, SVL 60.6 cm, head dorsum with dark blotches, nape scales with dark apices and dark-edged

ventrals on the throat. In all respects, it is a member of group B.

*Diemenia atra* Macleay, 1884a, was described from a collection received from J.A. Boyd of Ripple Creek, Ingham. No indication was given of the number of specimens on which the name was based, although only a single set of measurements and counts was presented. Two specimens have been identified as types: one (R131727; formerly B5941), presented to the Australian Museum by Macleay in 1885 as a type, the second (AM R31920, formerly Macleay Museum R708) originally in the Macleay Museum collection, identified on jar labels as a type. Of these two specimens, R31920 (Figs. 8C, 10) agrees more closely with Macleay's description (180 ventrals, 68 subcaudals, SVL 31 inches), and was designated lectotype by Wells and Wellington (1985). AM R31920 is a female with 177 ventrals, 69 subcaudals, SVL 78.5 cm, and the temporolabial bilaterally reaching the lower postocular, while AM R131727 is a male with 186 ventrals, 78 subcaudals and SVL 90.4 cm. Both lectotype and paralectotype are members of group B on scalation and size, and agree with this group in coloration (dark-edged ventrals on throat, body venter and dorsum uniform black). The locality given for both types in museum registers is Herbert River, which

Macleay (1884b) had used as an alternative description of the collector's residence.

*Diemenia maculiceps* was described from a single female specimen collected by Richard Semon from the Burnett River (Boettger 1898; Mertens 1967). I have not examined the holotype (Senckenberg Museum, Frankfurt 20498), but photographs and notes on coloration made by Dr H.G. Cogger (pers. comm.) clearly indicate that the type has the coloration of group B, in particular no transrostral bar, large dark blotches on the head shields and dark apices to scales on the nape. Further, the type locality is only within the known range of group B.

The holotype of *Demansia papuensis melaena* Storr, 1978 (WAM R47590; Figs 8D, 11), is a non-reproductive adult female from Katherine Farms, NT, collected by G. Gow. It has 211 ventrals, 85 subcaudals and SVL 101.7 cm, an evenly dark dorsum, small dark flecks on the head, and lacks dark

margins to the more anterior ventrals, and is clearly a specimen of group A.

## TAXONOMIC CONCLUSIONS

The concordance of variation in scalation, size and to a lesser extent coloration, together with the wide geographic overlap between the two forms, with morphological distinction maintained in sympatry, argues for the occurrence of two species. Geographic variation in each species is apparently continuous. On mainland Australia, there is no evidence for any population being either geographically isolated or consistently morphologically different, while New Guinea and Torres Strait island populations are morphologically completely consistent with the smaller Australian species. Thus, I do not recognise subspecies within either species. The earliest available name for the larger species with high scale counts (group A) is *Diemenia papuensis*, with *Demansia papuensis melaena* a junior synonym. The earliest available name for the smaller species with low counts (group B) is *Hoplocephalus vestigiatus*, with *Diemenia atra* and *Diemenia maculiceps* as junior synonyms. Although *D. vestigiata* has only recently and inconsistently been used as the available name for this taxon, *D. atra* has only been in use for the same taxon since 1974, prior to which the species was widely known as *D. olivacea*. I do not consider that use of the binomen *Demansia vestigiata* will cause nomenclatural instability any greater than the unavoidable confusion resulting from the restriction of *D. papuensis* to Australia.

The two taxa are most readily differentiated on ventral counts: 165–197, rarely above 193, for *D. vestigiata*, 198–228 for *D. papuensis*.

## IDENTITY OF MATERIAL DISCUSSED BY PREVIOUS AUTHORS

The taxonomic conclusions of this paper differ from the many solutions presented by previous authors. Many of the specimens

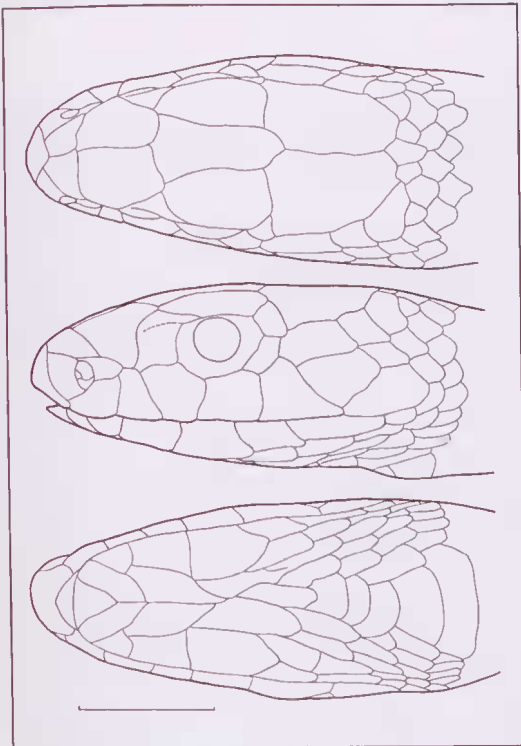


Fig. 7. Dorsal, lateral and ventral views of the head shields of the holotype of *Diemenia papuensis*. Scale bar = 10 mm.



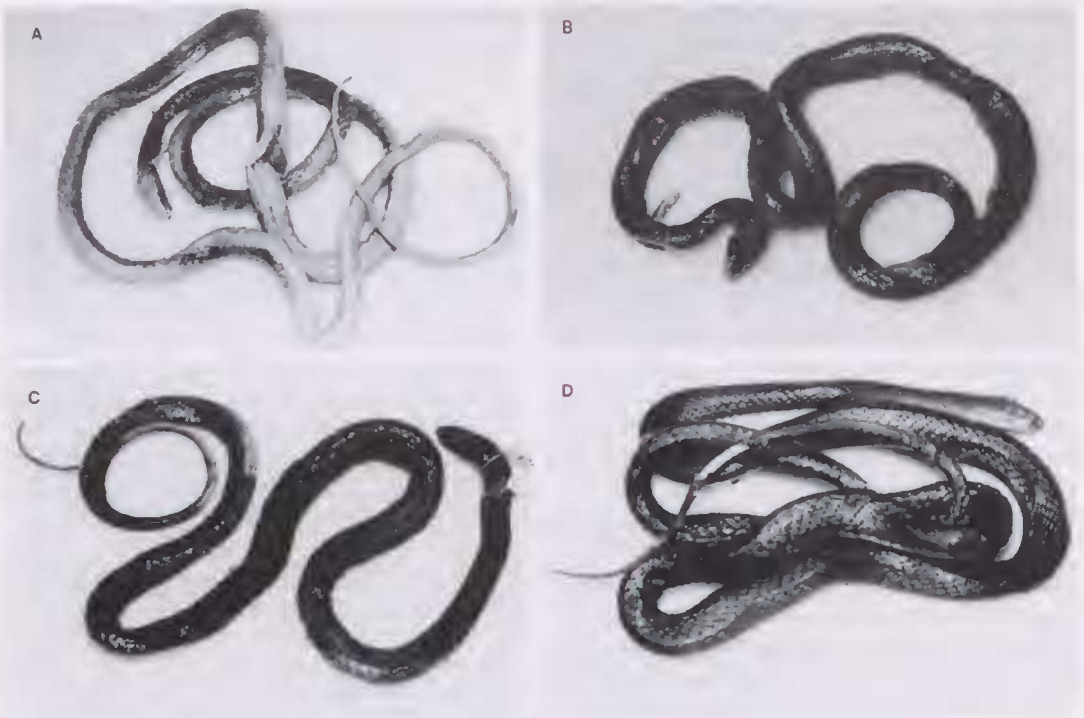


Fig. 8. A, holotype of *Diemenia papuensis*; B, holotype of *Hoplocephalus vestigiatus*; C, lectotype of *Diemenia atra*; D, holotype of *Demansia papuensis melaena*.

examined for this paper were also utilised by these earlier workers, and it is now possible to re-identify some of the material used in these studies.

Krefft (1869) reported specimens of *Diemenia psammophilis* and *D. olivacea* from Port Denison. One large early specimen of *D. papuensis* (AM R6097) is from Port Denison, and is likely to have been the basis of Krefft's record of *D. psammophilis* from this locality, as the counts and measurements he gives roughly correspond with this specimen. From his description of *D. reticulata* as common around Sydney, Krefft clearly applied this name to true *D. psammophilis*, and thus recognised this species as distinct from the large whip snakes.

Although none of the specimens used by Boulenger (1896) were examined in this study, the combination of locality and scale counts given allows the identification of many specimens. The New Guinea and Cape York specimens (Boulenger's a–d) of his variety B of *D. psammophilis*, in which he

placed *D. papuensis*, are clearly *D. vestigiata*. However, at least the second (f) of his Port Essington specimens of this 'variety' is *D. papuensis*. The other specimens (e, Port Essington; g, Daly River) may be *D. vestigiata* or *D. olivacea*. Among Boulenger's specimens referred to *D. olivacea*, a, b (north-eastern Australia) are most likely *D. vestigiata*, c (Port Darwin) may be *D. vestigiata* or *D. olivacea*, and d (Port Essington) is *D. papuensis*.

All of the specimens in the D.F. Thomson collection, now in the Museum of Victoria, were examined. The Cape York *D. olivacea* reported by Thomson (1935) are a mixture of *D. papuensis* and *D. vestigiata*.

Among the Worrell material lodged in the Australian Museum and Museum of Victoria as '*D. olivacea*' are specimens of *D. papuensis* from Mataranka (AM R13229, R13231), and one of *D. vestigiata* (MV D8626) from central Qld. As noted by Storr (1978), the only specimen of '*D. atra*' listed by Cogger and Lindner (1974) is a *D. papuensis*.

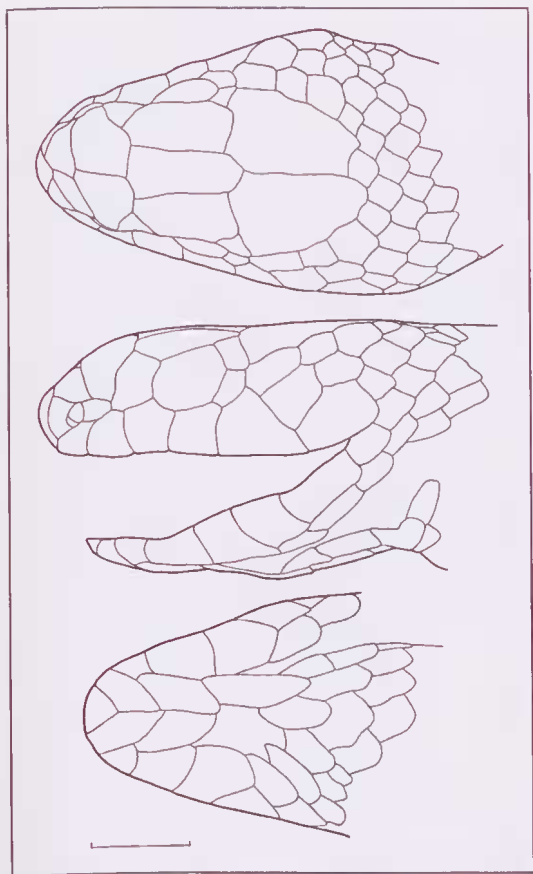


Fig. 9. Dorsal, lateral and ventral views of the head shields of the holotype of *Hoplocephalus vestigiatus*. Scale bar = 5 mm.

With the exception of WAM R47684 (Koolan I.), all specimens identified as *D. papuensis* and *D. vestigiata* (as *D. atra*) by Storr (1978) I consider correctly identified. The exception is a member of the *D. olivacea* complex, not *D. papuensis*. Further, three small individuals (WAM R21937, R24928, Katherine; R45688, 'Mt House') that Storr assigned to *D. olivacea* I re-identify as juvenile *D. papuensis*, hence including the central Kimberley in the range of this species for the first time.

Shine's (1980) account of the ecology of *D. atra*, based on the dissection of Australian Museum and Queensland Museum material, is clearly from a composite sample of *D. papuensis* and *D. vestigiata*, with the range of SVLs covering both taxa. However, the specimen he identified as *D. papuensis* (QM J8122) is correctly identified.

Thus, it is now clear that most previous studies were working with composite samples, usually small. This study emphasises the importance of examining large samples and using a range of collections to resolve taxonomic problems in snakes.

#### SPECIMENS EXAMINED

*Demansia papuensis*. AM R258, King Sound, WA; R3780, MV D4507, Pt Darwin, NT; AM R6097, Pt Denison, Qld; R9928, MV DT-D136, Roper River, NT; AM R10422, Cooktown, Qld; R13229, R13231, Mataranka, NT; R14033, Forrest River Mission, WA; R19105, R41869, Maningrida, NT; R20199, S of Katherine, NT; R31919, ?New Guinea (holotype of *Diemenia papuensis*); R41095, WAM R47590 (holotype of *Demansia papuensis melaena*), Katherine Farms, NT; AM

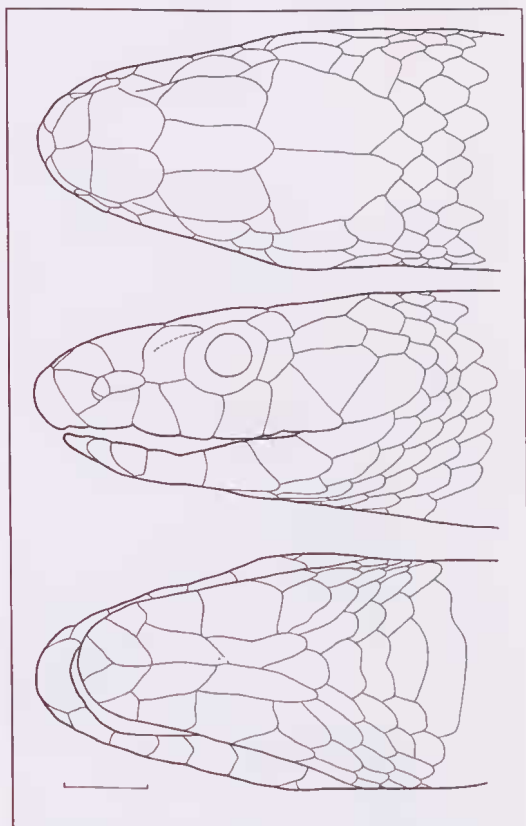


Fig. 10. Dorsal, lateral and ventral views of the head shields of the lectotype of *Diemenia atra*. Scale bar = 5 mm.

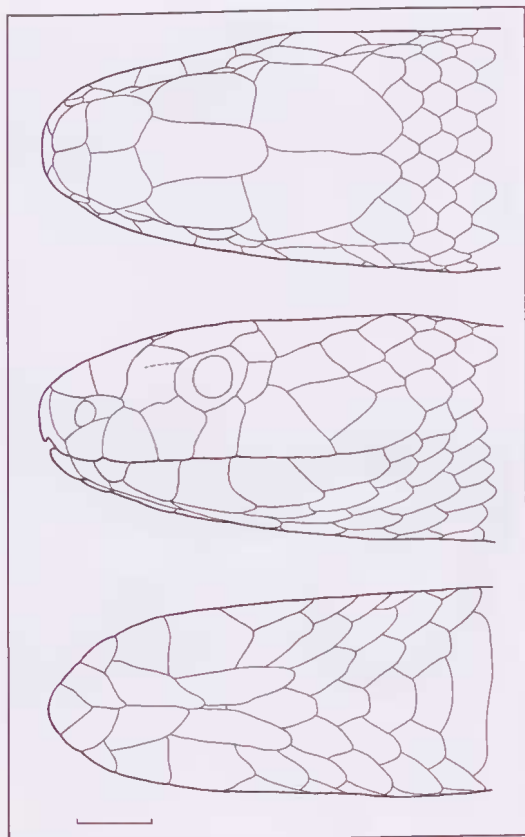


Fig. 11. Dorsal, lateral and ventral views of the head shields of the holotype of *Demansia papuensis melaena*. Scale bar = 5 mm.

R63378, 27.3 km E Georgetown, Qld; R79146, 8 km E Mareeba, Qld; R88831, Jabiluka Project Area, NT; R119699, Dimbulah, Qld; R139881, 11 km W Kununurra on Wyndham Rd, WA; R142895, 1 km W October Ck, NT; ANWC R543, between Mary River and South Alligator River on Cooida Rd, NT; R810, Numbulwar, Rose River, NT; R818, corner of McMillans Rd and Rapid Creek Rd, Rapid Ck, NT; R825, Tayimi, Bathurst I., NT; R946, Caranbirini Waterhole, 20 km NE Mimets Camp, NT; R1289, Mimets Base Camp, McArthur River, NT; MV R12811, QM J2976, Koolpinyah, NT; MV D8693-94, QM J33598, J50555, no locality; MV D10065-66, DT-D104-105, Roper River Mission, NT; R51889, Larrimah, NT; DT-D85, DT-D128, Yonko River, Qld; DT-D86-88, DT-D98-99, DT-D102, DT-D110, DT-D112, DT-D137-139, Milingimbi Mission, NT; DT-D106, Glyde River, NT; DT-D115,

lower Archer River, Qld; DT-D117, DT-D133, Yirrkala, NT; DT-D126, DT-D130, DT-D1168, DT-D1232, Barc Hill, Qld; NTM R156, R3720, Katherine Farms Rd, NT; R294, R5247, R16717, Howard Springs, NT; R2287, 9 mi W Katherine, Lower Farms Rd, NT; R3817, R3828, Katherine district, NT; R4727, Howard Springs Reserve, NT; R4729, R16775, WAM R16509, R21937, R23893, R23895, R24928, R26347, Katherine, NT; NTM R5814, Katherine, low level, NT; R5854, Berry Springs Reserve, NT; R6719, Ivanhoe Crossing, WA; R6882, Keep River, 35 km E WA border, NT; R7045, Kununurra, WA; R8266, El Sharana, NT; R8386, 11 km W Katherine on Stuart Hwy, NT; R9493, Victoria River by Victoria River Crossing, NT; R13149, Humpty Doo, NT; R14211, Vanderlin I., NT; R16575, R16621-22, R16624, R17234, Humpty Doo area, NT; R16823, 'Marrakai' Stn Rd, 5 km from Arnhem Hwy, NT; R17915, Jabiru East, NT; R20514, Cape Crawford area, NT; R20571, 'Bauhinia Downs', NT; R21008, Woolanang, NT; R32362, Berrimah, NT; R32369, Pine Creek, NT; R32370, R32372, Darwin, NT; R32373, Maria I., NT; NTM A/S R33, Gregory Ck, Qld; QM J2974, nr Pt Darwin, NT; J8122, Wenlock, Qld; J22344, Mt Molloy, Qld; J31513, Stoney Pt, Kungatham, nr Temple Bay, Qld; J33597, Pallarenda, Qld; J33599, 8 km S Elliot River between Bowen and Home Hill, Qld; J33600, Mudginburra, Qld; J38351, 'Silver Plains' HS, Qld; J39845, 1.5 km S Coen, Qld; J44972, 'Goldsborough', Lolworth Range, south face, Qld; J50269, Adel's Grove, 5 km E Lawn Hill NP, Qld; J50414, Lynd River, 'Amber', Qld; J51750, 20 km NE Coen, Qld; J51751, 60 km S Coen, Qld; J51230, Heathlands Rd, 2 km N 'Shelburne Bay' HS turnoff, Qld; J53825, Lockhart River, Qld; J54392, J54394, vicinity of Widdallion Ck, Qld; J57655, Musgrave-Pornpuraow Rd, Qld; J58745, Rossville, Qld; J58881, 13.8 km NE Normanton, Qld; J59377, Epping Forest, Qld; SAM R6640, Victoria River, NT; R29954, nr Humpty Doo, NT; WAM R144, Derby, WA; R11244, R12360, Wotjulum, WA; R11979-80, Kimberley Research Stn, WA; R13286-88, R22425, R28073, R64695-97, R125241-42, Kalumburu, WA; R13648, Wyndham, WA;



R22923, Kuri Bay, WA; R26673, Cape Don, NT; R45688, 'Mt House', WA; R46834, Prince Regent River Reserve, WA; R51202, Kimbolton Spring, WA; R51816, Stewart Range, 'Kimbolton', WA; R53714, Mitchell Plateau, WA; R55865-66, main dam site, Lake Argyle, WA; R60580, Camp Ck, Mitchell Plateau, WA; R74045, Gove, NT; R75125, 11 km W 'New Lissadell' HS, WA; R87272, 10 km NNE Kununurra, WA; R97960, nr Mt Barnett, WA.

*Demansia vestigiata*. AM R3335, MV D1936, D4430, D9016-17, NTM R3560, R16623, QM J206 (holotype of *Hoplocephalus vestigiatus*), J353, J1584-86, J19849-50, J47357, J50562, no locality; AM R5845, R31920 (leetype of *Diemenia atra*), R131727 (paralectotype of *Diemenia atra*), QM J1593-94, Herbert River, Qld; AM R6205, Eidsvoll, Qld; R6488, Homebush, Mackay, Qld; R6938, Mackay district, Qld; R7611-12, Mekeo, 60 mi NW Port Moresby, PNG; R8906, Caloden Bay, Centre I., Pelew Is., NT; R9024, Coorooman, Qld; R12459-63, northern Australia; R14032, R14034, Port Keats Mission, NT; R14599, R14625, Laloki River, PNG; R16737, 'Silver Plains', Qld; R17079, Gregory Springs via Hughenden, Qld; R25823, R115352-53, QM J25884, J32903, Port Moresby, PNG; AM R30716, R66763, R93233, R121152, MV D14435, Wipim, PNG; AM R37868, 10 mi S Coen, Qld; R40276, Cannon Hill, NT; R40847, Tully, Qld; R40848, QM J26088, J40700, J48963, Gladstone, Qld; AM R44533, Karumba, Qld; R49833, R62738, Burnett Heads, Qld; R54201, Finehes Bay, Cooktown, Qld; R54918, 30 km upstream, Liverpool River, NT; R55039, 3 km S Batten Pt, NT; R56661, 114 km N Cairns on Cooktown Rd, Qld; R56662, Annan River crossing, southeast of Cooktown, Qld; R57054, 5 mi S Gladstone, Qld; R59063, R59110, QM J37944, J43427-28, Badu I., Qld; AM R59888, 4 mi N Yalboroo on Bruce Hwy, Qld; R59889, 24 mi N Proserpine, Qld; R62018, about 20 km from Weipa on Mapoon Rd, Qld; R63727, Crooked Creek at Gulf Hwy, 34.5 km W Georgetown post office, Qld; R65905, Isis River crossing on Bruce Hwy, 13 km E Childers, Qld; R66211, QM J16821, Mitchell River Mission, Qld; AM R69971,

Kerry Head, Proserpine, Qld; R79262, ANWC R350, NTM R315, R32361, Beatrice Hill, NT; AM R81473, just below Ross River Dam, west of Townsville, Qld; R81474, rubbish tip *ca* 4.7 km W Cooktown post office via airport rd, Qld; R81475-76, Bowen tip, Qld; R82541, R85720, Lorim Pt, Weipa, Qld; R82559, abandoned Mapoon Aboriginal Settlement, north of Weipa, Qld; R82587, R82589, QM J52813, Thursday I., Qld; AM R84222, northeast Qld; R86833, Kapa Kapa, 50 mi SE Port Moresby, PNG; R88573, Jabiluka Project Area, NT; R91627, R94368, Weipa district, Qld; R92530, Ord River Diversion Dam, WA; R93715, Ross River, vicinity of Kelso, 14 km from Townsville, Qld; R97430, NTM R17913, Jabiru East, NT; AM R97515, Magela Crossing on Oenpelli Rd, 2 km N 'Mudginberri' Stn, NT; R97539, 1 km S Mieea Ck crossing on Jim Jim Rd, NT; R105280, opposite end of airstrip, Coen Rd from Weipa, Qld; R107091, 11 km E Weipa on Coen Rd, Qld; R110339, R110359, R110374, QM J3638, SAM R12784, WAM R55615, Townsville, Qld; AM R111360, Berrimah Farm, NT; R112425, Arnhem Hwy, vicinity of Jabiru, NT; R113357, Mt Morgan tip, Qld; R114142, Maningrida, NT; R119456, Darwin, NT; R119698, Dinah Lagoon, Dinah I., Staaten River, Qld; R121994, Moitaka, Port Moresby, PNG; R127965, Mt Carbine, Qld; R141689, 8 km E South Alligator River on Arnhem Hwy, NT; ANWC R170, Mackay Harbour, Qld; R814, Humpty Doo Rd, between ricefields and CSIRO Stn, NT; R823, 1 mi NW Fogg Dam, Humpty Doo, NT; R1014, Maprik, PNG [in error]; R1421, Yeppen, 3 mi S Rockhampton, Qld; R2698, 30 mi S Rockhampton, Qld; R2784, Normanton, Qld; R5279, eastern McIlwraith Range lowlands, Qld; R5419, Shoalwater Bay Army Training Reserve (22°24'S 150°12'E), Qld; R5458, Shoalwater Bay Army Training Reserve (22°45'S 150°18'E), Qld; R5481, Shoalwater Bay Army Training Reserve (22°24'S 150°16'E), Qld; MV R12809, R12869, NTM R808, Oenpelli, NT; MV R12810, D8477, Darwin, NT; R12861, Cape York, Qld; D4672, D4732, D4825, PNG; D4681, Daintree River, Qld; D8684, QM J7573, J15878, Rockhampton, Qld; MV

D5903, Bora Bada, PNG; D8443, Mornington I., Qld; D8467, D8475-76, Finnis Lake, NT; D8626, central Qld; D8971, Cleveland, Qld; D49836, D49896, Awaba, PNG; DT-D89, DT-D97, DT-D100-101, DT-D103, DT-D111, WAM R13532-33, Milingimbi Mission, NT; MV DT-D90, nr Cape Direction, Qld; DT-D91-94, DT-D107, DT-D113-14, DT-D119, DT-D121-125, DT-D131, DT-D1169, lower Archer River, Qld; DT-D96, nr Pt Musgrave, Qld; DT-D95, QM J48122, Gympie, Qld; MV DT-D108, lower Archer River (register) or lower Watson River (label), Qld; DT-D109, second Red Rocky Point, Qld; DT-D127, lower Watson River, Qld; DT-D129, DT-D134-35, Katji Lagoon, NT; NTM R919, Mareeba, Qld; R987, Edward River Mission, Cairns, Qld; R1174, Berrimah, NT; R1940, Stuart Hwy, Berrimah, NT; R3433, 27.0 km E Mt Bundy turnoff on Arnhem Hwy, NT; R3452-53, Harrison Dam, 29 km NE Noonamah, NT; R6215, Gunn Point Rd, Howard Springs, NT; R8373, nr river, Howard Springs, NT; R12479, Fogg Dam, NT; R16620, R16625, Humpty Doo, NT; R16822, Adelaide River floodplain, Arnhem Hwy, NT; R17060, 2 km E Adelaide River on Arnhem Hwy, NT; NTM A/S R492-494, Borroloola, NT; QM J309, Brisbane, Qld; J359, Coongoola district, Colosseum, Qld; J374-75, Noosa Heads, Qld; J604, J7073, Cape York, Qld; J1595, Cardwell, Qld; J1782, Pt Darwin, NT; J2544, J22781, SAM R18625, Bundaberg, Qld; QM J2572-73, 30 mi E Darwin, NT; J3572, Belmont, Brisbane, Qld; J4195, Watalgan, Qld; J5677, Homebush Rd, Glendora, Mackay; J6948, Konedobu, Pt Moresby, PNG; J6954, Base area, lower level, PNG; J7864, J7871, J8123, Wenlock, Qld; J10028, Bucasia, nr Mackay, Qld; J10359, Atherton, Qld; J10710, J15810, J40344, Proserpine, Qld; J13445, Gulliver, Townsville, Qld; J13515, Toorbul, Qld; J13576, nr Townsville, Qld; J14335, 5 km S Iron Range, Qld; J14336-37, Browns Ck, Cape York, Qld; J17672, 26 km N Gladstone on Bruce Hwy, Qld; J18355, 9.6 km N Bundaberg on Rosedale Rd, Qld; J18535, 3.2 km S Tiaro on Bruce Hwy, Qld; J20429, Mt Brisbane, Esk, Qld; J21791, J21797, J21783, Humpty Doo district, *ca* 64 km SE

Darwin, NT; J21964, J25499, 'Pine Valley', Brooweena, Qld; J21970, Broadwater Ck, via Baffle Ck, Qld; J22033, Darwin area, NT; J22149, Mirani, Qld; J22300, J47301, Gympie district, Qld; J22577, 8 km W Woodgate, Qld; J22618, Pt Curtis Rd, Rockhampton, Qld; J23199, Millaroo, nr Ayr, Qld; J23213, Marina Plains - Musgrave, *ca* 10 km from Musgrave, Qld; J25698, Coolum, Qld; J26665, 26.1 km NW Townsville on Bruce Hwy, Qld; J28070, 0.5 km N Lockhart River, Qld; J28071, 2 km N Lockhart River, Qld; J28447, Mackerel St, Tin Can Bay, Qld; J28787, 2 km N Lockhart River community, Qld; J28789, nr school, Lockhart River community, Qld; J28909-10, 10 km SE Paluma turnoff on Bruce Hwy, Qld; J29082-84, Shoalwater Bay Army Reserve, Qld; J32286, Croydon, Qld; J32290, Shute Harbour, Qld; J32898, Korobosea, Pt Moresby, Qld; J33501, Toolara SF, Qld; J35171, Takura, nr Maryborough, Qld; J35172, Hervey Bay, Qld; J36033, Hervey Bay (urban), Qld; J36081, Booloumba Ck headwaters, Connondale Ranges, Qld; J37052, W of Anakie, Qld; J37581, J38213, Pt Stewart, Qld; J37584, Peach Ck, 16 km NE Mt Croll, Qld; J37585, Lankelly Ck, 10 km NE Coen, Qld; J37586, Rocky River, 8 km SW mouth, Qld; J37587, 3 km SE Coen, Qld; J37610, 5 km SW 'Breakfast Creek' HS, Qld; J39680, 8 km N Camp Beagle on Watson River Rd, Qld; J39844, York Downs, 50 km E Weipa, Qld; J40230, N of Camp Beagle, *ca* 40 km N Aurukun, Qld; J40279, Yaamba, Shoalwater Bay area, Qld; J40767, Cooktown, Qld; J40935, Harrisville, Qld; J41395, N Stradbroke I., Qld; J41530, Maryborough area, Qld; J44592, 'Warrawee', Qld; J44961, J44984, 'Toomba', Qld; J44971, J44982, 'Hillgrove', Qld; J44979, 'Southwick West', Qld; J44983, J44986, 'New Moon', Qld; J46811, junction of Catfish Ck and Calliope River, Qld; J46864, Fletcher Ck mouth, Burdekin River, Qld; J47297, Winfield via Gympie, Qld; J47410, Durong, Qld; J48663, 29 Ward St, Tewantin, Qld; J48681, Kinka Beach, N of Emu Park, Qld; J49836, Nelly Bay, Magnetic I., Qld; J49940, Boondoomba, via Proston, Qld; J50557-58, J50561, J50563-64, J50566-67, J50570,



J50575, Pallarenda, Townsville, Qld; J50559, Townsville Town Common, Qld; J50560, Pallarenda Rd, Pallarenda, Qld; J50565, Mt Elliot turnoff, S of Townsville, Qld; J50568, 'Jerona', S of Townsville, Qld; J50569, Cape Cleveland, Qld; J50571, J51978, 'Inkerman', Qld; J50572, Cranbrook, Townsville, Qld; J50573, Bohle River, Hervey Range Rd, Qld; J50574, Greenvale area, NW of Townsville, Qld; J50576, Mt Elliot, Qld; J52851, 11.2 km N Marceba, Qld; J52858, Gregory River, 16 km S Burketown, Qld; J53087, MacDonald Point, Shoalwater Bay, Qld; J53639, 1 km N site 12, Shoalwater Bay, Qld; J53640, Plot 11, nr site 12, Shoalwater Bay, Qld; J55227, Cape Hillsborough Rd, Qld; J55228, Rabbit I. NP, Qld; J57044, corner Sugarloaf and Strathdickie rds, via Proserpine, Qld; J57098, 'Warrill View' (QDPI Animal Genetics Centre), Qld; J57654, 'Lochnager' outstation, Qld; J57656, 'Rutland Plains' HS, Qld; J58149, Peak Crossing, Qld; SAM R1102, 'Minnie Downs', Qld [in error]; R34265, Jabiru airstrip, NT; R34351, James Cook University, Qld; R35462-63, Kununurra, WA; WAM R10242, Ivanhoe, WA; R13448, Wyndham, WA; R13509, Yirrkala, NT; R22347-48, R29914, Kimberley Research Stn, N of Kununurra, WA; R25089, 60 km SSE Wyndham, WA; R55849, Routh Ck, 30 km E Georgetown, Qld; R56160, 2 km W Croydon, Qld; R57865, nr Laura, Qld; R71209, 10 km N Cooktown, Qld; R75539, 3 km SSE Kununurra, WA; R75552, 6 km NE Kimberley Research Stn, WA.

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